BIRD NESTING ECOLOGY IN A FOREST DEFOLIATED BY GYPSY MOTHS

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ABSTRACT.—Acadian Flycatcher (*Empidonax virescens*, n = 55), Indigo Bunting (*Passerina cyanea*, n = 60), Eastern Towhee (*Pipilo erythrophthalmus*, n = 41), and Wood Thrush (*Hylocichla mustelina*, n = 62) nests were monitored during 1995–1996 in the eastern panhandle of West Virginia, at the Sleepy Creek Wildlife Management Area. The objective of this study was to relate the outcomes of bird nests to surrounding habitat characteristics in an area that experienced heavy tree mortality from prior defoliation by the gypsy moth (*Lymantria dispar*). Large (> 22.9 cm dbh) standing snags in the nest patch were not associated with nest failure for any of the four bird species. Very large diameter (> 38.1 cm dbh) live trees and snags and reduced canopy cover increased the chances of Brown-headed Cowbird (*Molothrus ater*) parasitism only for Indigo Buntings. Nest patches of all four species differed in vegetation characteristics from random plots in similar habitat, typically by having greater densities of species' preferred nesting substrate in the nest patch. Gypsy moth defoliation, which can result in an increase in snags and opened canopy, is not likely to be a devastating ecological event for shrub and sub-canopy nesting avian species, and can create more nesting habitat for many species that use a dense forest understory. *Received 18 Jan. 2000, accepted 22 June 2000*.

The gypsy moth (Lymantria dispar) was introduced to North America around 1869 and has become an important forest pest in the eastern United States (Liebhold 1990). Gypsy moth defoliation alters the structure and composition of the forest by causing tree mortality (Campbell and Sloan 1977, Houston and Valentine 1977, Bell 1997). Oaks (Quercus spp.) in particular are a preferred food item in the East (Twery 1991, Liebhold et al. 1995). To limit both the spread and the damage caused by gypsy moths, spraying of pesticides, primarily Bacillus thuringiensis and diflubenzuron, has been widespread. Both Bacillus thuringiensis and diflubenzuron have detrimental effects on birds (Cooper et al. 1990, Rodenhouse and Holmes 1992, Sample et al. 1993a, Whitmore et al. 1993) through the reduction of non-target Lepidoptera larvae (Sample et al. 1993b, Sample et al. 1996, Butler et al. 1997), an important food source during the breeding season.

Knowing that pesticide use is detrimental to bird populations, it is equally important to assess the possible deleterious effects of inaction on forest birds; that is, when no efforts

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are taken to control gypsy moth populations and they are left to run their course. Following a heavy gypsy moth outbreak, populations of many ground, shrub, subcanopy, and snag-using bird species increased (Bell 1997, Bell and Whitmore 1997a). However, the relationship between density of a species and the quality of the habitat is not always clear. In some cases, high animal densities indicate high quality habitat and in other cases they do not (Vickery et al. 1992, Van Horne 1983, Hunt 1996, Holmes et al. 1996). In avian conservation, it is necessary to determine which habitat characteristics affect survival and nesting success (Martin 1992), particularly in light of concerns about population declines of many species of migratory landbirds (Robbins et al. 1989, Askins et al. 1990).

There has been speculation that the opening of the forest canopy and the presence of snags, features created by gypsy moth damage, can create conditions favorable for Brown-headed Cowbird (Molathrus ater) parasites and nest predators (Robbins 1979, Yahner and Wright 1985, Thurber et al. 1994, Rotenberry et al. 1995). Snags may provide perch sites from which cowbirds could locate nests in which to lay their eggs. It also is possible that avian predators could use them to search for nests. However, in forested landscapes, some researchers have found no relationship between number of snags surrounding the nest patch and parasitism (Brittingham and Temple 1996).

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It is necessary to monitor nests in order to better understand the dynamics of bird nesting ecology in a defoliated forest. In this study we focused on four bird species common to the study area: Acadian Flycatchers (Empidonax virescens), Indigo Buntings (Passerina cyanea), Eastern Towhees (Pipilo erythrophthalmus), and Wood Thrushes (Hylocichla mustelina). Numbers of Indigo Buntings, Eastern Towhees, and Wood Thrush increased after gypsy moth defoliation and tree mortality, while Acadian Flycatchers declined (Bell 1997, Bell and Whitmore 1997a, Bell and Whitmore 1997b). Our objectives were to describe the nest-site characteristics of birds in a gypsy moth-impacted forest and to determine which habitat features (if any) differed between parasitized and unparasitized nests, successful and unsuccessful nests, and nest patches and random patches in similar habitat.

STUDY AREA AND METHODS

This study was conducted within the Sleepy Creek Wildlife Management Area (WMA; formerly Sleepy Creek Public Hunting and Fishing Area; 39° 44' N, 78° 18' W), an 8000 ha area located on Sleepy Creek and Third Hill Mountains (elev. 240-662 m) in Morgan and Berkeley counties, West Virginia. This study was designed to be mensurative (as opposed to manipulative) in that plots were established to compare experimental units over space or time (Hurlburt 1984, Cooper et al. 1999). We did not believe that comparing nests at Sleepy Creek WMA to undefoliated control sites was feasible. To prevent gypsy moth defoliation and subsequent tree mortality, agents such as Bacillus thuringiensis and Dimilin, both of which have been shown to have adverse effects on songbirds would have to be used. To establish plots in areas far enough away from Slcepy Creek WMA so as to be totally unaffected by gypsy moths would introduce site biases in vegetation structure and composition and their coneomitant bird faunas.

The Sleepy Creek WMA area lies within the rolling Ridge and Valley province and is typical of the oakhickory forests of the region. Tree species common to the area include red, chestnut, and white oaks (Quercus rubra, Q. prinus, Q. alba), hickories (Carya spp.), yellow poplar (Liriodendron tulipifera), red maple (Acer rubrum), black bireh (Betula lenta), sassafras (Sassafras albidum), black gum (Nyssa sylvatica), and pitch pine (Pinus rigida). Sleepy Creek WMA is maintained by the West Virginia Division of Natural Resources and no efforts were taken during this study to control gypsy moth populations in our study plots. Heavy defoliation oceurred in 1987 and 1988 as gypsy moth populations reached outbreak levels (Cooper et al. 1993, Bell 1997) and defoliation levels fluctuated after that (Bell 1997). Bird populations and habitats were monitored before (1984–1986), during (1987–1988), and after (1989–1996) the initial severe outbreak. During the time nesting birds were monitored (1995– 1996), gypsy moth caterpillars were rarely observed and defoliation was negligible. The amount of damage to the area after defoliation varied widely. By the postoutbreak period, some sites within Sleepy Creek WMA lost up to 80% of their pre-deloliation number of large oak trees (the dominant tree in the area) while others were undamaged and increased in the number of large oaks (Bell 1997).

Vegetation sampling.—Seven transects, each 2 km in length, were established at the study site. Two transects were placed along each elevational gradient (ridgetop, mid-slope, and valley) of the eastern slope of Sleepy Creek Mountain to represent a uniform sample of the locations on the mountain. The seventh transect was along the western midslope of Third Hill Mountain, which lies parallel to Sleepy Creek Mountain. Six eireular (125 m radius) permanent plots were placed along each transect, for a total of 42 plots. Within every plot, 5 permanent 0.04 ha subplots were placed, for a total of 210 subplots. One subplot was always located at the plot center and one was randomly located within each of the four quadrants of the 125 m plot. These subplots served as a random sample of the vegetation structure and composition of the area. At each subplot, vegetation (e.g., canopy cover, shrub eover, and number, size, and species of trees) was sampled similar to the manner of James and Shugart (1970). There were 5 sampling points in each cardinal direction spaced 2.26 m apart, for a total of 20 sampling points per 0.04-ha subplot. At each sampling point, ground cover and vegetation were recorded using a sighting tube with a wire cross-hair at the end. The observer sighted vertically through the tube, first down, then up, and vegetation that intersected the eross-hairs, from the ground to the top of the canopy, was recorded. First, presence/absence of canopy above 3 m was recorded as total canopy cover. If foliage 0-3 m was intercepted by the cross-hairs, it was recorded by Genus or species and counted as shrub eover. At cach sampling point, every intersection of the vegetation with the cross-hair counted as 5%, so values for each variable ranged from 0-100% at each subplot. The number and diameter at breast height (dbh) of each species of tree (any woody plant > 3 m in height) within the subplot were measured using a modified Biltmore stick (James and Shugart 1970).

Nest monitoring.—Nests of four bird species (Acadian Flycatchers, Indigo Buntings, Eastern Towhees, and Wood Thrushes) were loeated and monitored. These species were chosen because all four were common to the area and it was believed that their nests could be found in large enough numbers for statistical analysis. Areas within and around the 42 plots were searched intensively for nests. All nests found within the study area were monitored every 3–4 days following the protocols of the Breeding Biology Research and Monitoring Database (BBIRD) program (Martin et al. 1996). After each nesting attempt was completed, vegetation was sampled in a 0.04 ha plot (the nest patch) centered on the nest in the same manner as each of the 210 vegetation sampling subplots were measured. Thus, nest patches chosen by birds could be compared with the vegetation structure and composition of the study site. Nest patches also were compared between successful and unsuccessful, and parasitized and unparasitized nests for each of the four species separately.

Statistical analyses.—Nesting success was calculated using the Mayfield method (Mayfield 1961, 1975; Johnson 1979), a procedure with widespread use (Ralph et al. 1993, Martin et al. 1996). For comparison between successful/unsuccessful and parasitized/unparasitized nests, seven habitat variables were chosen based on habitat structural characteristics that could potentially affect nesting success (Anderson and Storer 1976, Martin 1993, Thurber et al. 1994, Brittingham and Temple 1996, Barber and Martin 1997). These were number of live trees (> 3 m tall) in three sizeclasses (0-7.6 cm dbh, 22.9-38.1 cm dbh, and > 38.1cm dbh), number of large dead trees in two size-classes (22.9-38.1 cm dbh and > 38.1 cm dbh), percentage cover of overhead canopy (foliage > 3 m in height), and percentage foliage in the shrub layer (0-3 m tall). The same seven variables and five additional variables (percent cover of the five most common non-herbaccous vegetation species in the nest patch shrub layer) were used to determine if there were any differences between nest patches and random plots for each species. Because nests were found in 1995 and 1996, data from vegetation plots from both years were used. Our goal was to determine microhabitat selection, so when comparing nest plots to random plots, we used only plots of the same general habitat type to find out what nest features the birds were choosing within a generally suitable area. These plots were selected by only using vegetation subplots from plots where each species was detected singing in either year of the study (Bell 1997). To determine which vegetation species were most commonly used for nest placement, the number of nests was tallied by vegetation type for each bird species.

To reduce the number of variables we assessed the association between each habitat variable and the dichotomous outcome of a nest in a univariate logistic regression model for each individual bird species. Variables that had a P value of less than 0.25 were retained for use in a stepwisc logistic regression model (Hosmer and Lemeshow 1989). Stepwise logistic regression (Hosmer and Lemeshow 1989, Menard 1995, SAS 1995) was used to determine which habitat variables were associated with the dichotomous outcome of a nest. Significance level to stay in the model was $\alpha = 0.05$. Although stepwise procedures may result in an elevated chance of a Type I error, the goal of stepwisc procedures was to identify the most parsimonious set of variables that adequately describe the outcome variable (Hosmer and Lemeshow 1989). Furthermore, it has been suggested that larger values of α are reasonable when specific relationships are anticipated a

priori, as is the case here (Kupper et al. 1976). To avoid problems with collinearity among variables, all independent variables used in each of the models had a Pearson correlation coefficient of less than 0.5. Statistical analyses were performed using The SAS System, Version 6.12 (SAS Institute Inc. 1996).

RESULTS

During the summers of 1995-1996, we found 55 Acadian Flycatcher, 60 Indigo Bunting, 41 Eastern Towhee, and 62 Wood Thrush nests (Table 1). Comparisons of habitat characteristics between parasitized and unparasitized nests of each species revealed that habitat variables differed only for Indigo Buntings. Parasitized Indigo Bunting nests were more likely to have less canopy cover ($61 \pm 5.2\%$ vs. 72 \pm 3.3%, Wald χ^2 = 4.51, P = 0.03, odds ratio = 1.39 for a -10% change), more large live trees (> 38.1 cm dbh; 0.9 ± 0.1 vs 0.5 ± 0.1 ; Wald $\chi^2 = 5.29$, P = 0.02; odds ratio = 4.53), and large (> 38.1 cm dbh) snags (0.9 \pm 0.2 vs 0.4 \pm 0.1; Wald $\chi^2 = 4.30$, P = 0.03; odds ratio = 2.14) in the nest patch than unparasitized nests (total nests n = 60). Only Wood Thrushes had significant differences in habitat surrounding successful and unsuccessful nests. Successful nests had more foliage cover in the shrub layer (0-3 m) in the nest patch than failed nests (76 \pm 3.0% vs 66 \pm 3.2%, n = 62; Wald $\chi^2 = 4.37$, P = 0.03; odds ratio = 1.4 for a +10% change).

All four bird species' nest patches differed in specific habitat characteristics from surrounding similar habitat. Eastern Towhee nest patches were more likely to have more grapevine (Vitis spp.) cover (6.0 \pm 1.3% vs 3.1 \pm 0.4%; Wald $\chi^2 = 7.29$, P = 0.0069; odds ratio = 1.6 for a -10% change) fewer 0-7.6 cm dbh saplings $(31.7 \pm 3.2 \text{ vs } 44.6 \pm 1.4; \text{ Wald}$ $\chi^2 = 13.45, P < 0.001;$ odds ratio = 0.96), and large-diameter (>38.1 cm dbh) live trees $(0.7 \pm 0.1 \text{ vs } 1.3 \pm 0.1; \text{ Wald } \chi^2 = 6.40, P$ = 0.011; odds ratio = 0.63) than random plots in similar habitat (n = 421). Indigo Bunting nest patches were more likely to have more blackberry (*Rubus* spp.; 50.2 ± 3.2 vs $20.9 \pm$ 1.9; Wald $\chi^2 = 36.89$, P = 0.001; odds ratio = 1.53 for a +10% change) and hickory shrub cover (8.4 \pm 1.0 vs 6.1 \pm 0.6; Wald $\chi^2 = 4.48$, P = 0.0342; odds ratio = 1.65 for a +10% change) with fewer 0-7.6 cm dbh saplings $(21.0 \pm 1.8 \text{ vs } 39.8 \pm 2.3; \text{ Wald } \chi^2 = 13.11,$ P < 0.001; odds ratio = 0.96) and large-di-

Variable	Acadian Flycatcher	Indigo Bunting	Eastern Towhee	Wood Thrush
# nests	55	60	41	62
# exposure days	866.5	626	362.5	778
# successful nests	30	33	15	26
# failed nests	25	27	26	36
Mayfield % success	47%	39%	19%	32%
Mayfield daily predation rate	2.8%	4.3%	7.1%	4.6%
# fledglings per successful nest	2.8	2.5	2.7	3.2
# parasitized nests (%)	8 (15%)	18 (30%)	3 (7%)	15 (24%)
# host young fledged in nests with Brown-headed Cowbird nes-	0		0.7	2.2
tlings # host young fledged in nests without Brown-headed Cowbird	0	1.8	2.7	2.3
nestlings # Brown-headed Cowbird fledg-	2.8	2.8	2.8	3.3
lings per successful host nest # Brown-headed Cowbird fledg-	0	0.28	0.03	0.13
lings per failed host nest	0.12	0.03	0	0

TABLE 1. Productivity estimates for Acadian Flycatchers (*Empidonax virescens*), Indigo Buntings (*Passerina cyanea*), Eastern Towhees (*Pipilo erythropluthalmus*), and Wood Thrushes (*Hylocichla mustelina*) in a forest defoliated by gypsy moths (*Lymantria dispar*) in West Virginia, 1995–1996.

ameter (>38.1 cm dbh) live trees (0.6 \pm 0.2 vs 1.4 \pm 0.1; Wald χ^2 = 7.53, P = 0.0061; odds ratio = 0.53, n = 261) Wood Thrush nest patches were more likely to have more canopy cover (88.0 \pm 1.3 vs 83.0 \pm 0.8; Wald χ^2 = 7.24, P = 0.0071; odds ratio = 1.42 for a +10% change), greater witch hazel (Hama*melis virginiana*) shrub cover $(13.3 \pm 2.6 \text{ vs})$ 6.3 \pm 0.6; Wald χ^2 = 12.63, P < 0.001; odds ratio = 1.34 for a +10% change), and fewer of the largest live trees (> 38.1 cm dbh; 0.8 \pm 0.1 vs 1.2 \pm 0.1; Wald χ^2 = 7.09, P = 0.0078; odds ratio = 0.67, n = 442). Acadian Flycatcher nest patches were more likely to have more witch hazel (15.5 \pm 2.3 vs 9.8 \pm 1.1; Wald $\chi^2 = 10.95$, P < 0.001; odds ratio = 1.44 for a $\pm 10\%$ change) and black birch (Betula lenta) (9.9 \pm 1.6 vs 5.4 \pm 0.7; Wald $\chi^2 = 5.55, P = 0.0184$; odds ratio = 1.42 for a +10% change) shrub cover, fewer live trees $(> 22.9-38.1 \text{ cm dbh}; 1.9 \pm 0.2 \text{ vs } 2.3 \pm 0.2;$ Wald $\chi^2 = 4.30$, P = 0.0379; odds ratio = (0.81) and fewer (0-7.6) cm dbh saplings (42.9) \pm 2.4 vs 55.0 \pm 2.0; Wald χ^2 = 13.29, P < 0.001; odds ratio = 0.97) than random plots (n = 220).

Most Acadian Flycatcher nests we found were in witch hazel (42%), followed by red maple (22%), black birch (16%), and dogwood (13%). Eighty percent of Indigo Bunting nests found were in *Rubus* spp. Eastern Towhee nests were primarily found in grapevine (27%), *Rubus* spp. (17%), greenbriar (12%), and mountain laurel (12%). Wood Thrush nests were found primarily in witch hazel (32%), black gum (19%), and red maple (19%).

DISCUSSION

We found no association between large snags in the nest patch and higher nest predation for the four species in this study. We found that Indigo Bunting nests at sites with less canopy cover, but with large diameter trees and snags were parasitized more than nests with a more closed canopy and fewer large-diameter trees and snags. Because this effect was seen with both live and dead trees, the important factor appears to be the size of the tree in an open area, regardless of whether the tree is live or dead. In more open habitat. the presence of emergent live trees has been noted to increase the probability of parasitism (Anderson and Storer 1976, Johnson and Temple 1990). Clearcuts with snags were found to have more Brown-headed Cowbirds than those with no snags (Dickson et al. 1983), further indicating that large trees in open stands may be used by cowbirds. The structure of the understory also may have compounded the perch effect. Eighty percent of the Indigo Bunting nests we found were in blackberry (or in small seedling trees mixed in with blackberry), which is shade intolerant and was found in large canopy gaps on drier sites within the study area. In the canopy gaps where we typically found Indigo Bunting nests, there were significantly fewer small trees than in the surrounding habitat. Thus, either a large diameter snag or live tree, where the canopy was generally open with no subcanopy could provide a good view of the understory where these birds were nesting.

None of the other species we examined had higher parasitism rates when large trees or snags were in the nest patch. As suggested by other researchers (Barber and Martin 1997, Brittingham and Temple 1996), snags may provide a view above the canopy but not below the canopy where nest-building of subcanopy species, such as Wood Thrushes and Acadian Flycatchers occurred. Therefore, a large snag surrounded by a dense subcanopy of saplings may not provide a good nest locating perch for cowbirds.

Habitat characteristics between successful and failed nests were different only for Wood Thrushes. Successful Wood Thrush nests had more foliage cover in the shrub layer (cover 0–3 m high) in the nest patch than failed nests. Wood Thrush nests are bulky compared to many passerine nests and when placed in an understory sapling tree are often visible to humans and possibly to potential predators. Dense foliage cover in the nest patch of a Wood Thrush nest may lessen the chances of detection by predators by obscuring it or decreasing scent transmission.

Acadian Flycatchers and Wood Thrushes placed most of their nests in witch hazel. This low spreading shrub provides nest placement sites and adequate concealment. Both species' nests were found in areas with a closed canopy (approximately 88% closure) and shade tolerant witch hazel in the understory. Although successful nests did not differ from failed nests in the amount of shrub level witch hazel, nest patches for both species had significantly more witch hazel cover in the shrub layer than random vegetation plots. A similar pattern was seen for Indigo Buntings and Eastern Towhees, both of which had significantly more foliage cover of their preferred nesting substrate (*Rubus* spp. and *Vitis* spp. respectively) in the nest patch than did random vegetation plots. That birds had more of the plants they chose for nesting in the nest patch than nearby random patches provides support for the idea that birds may select nest patches with more potential nest sites in order to reduce predator search efficiency (Martin 1993, Farnsworth and Simons 1999).

Three of the four species we examined had significantly fewer saplings in the nest patch than in the surrounding habitat. Indigo Bunting and Eastern Towhee nests were primarily found in vining plants [e.g., greenbriar (Smilax spp.), grapevine, Virginia creeper (Parthenocissus quinquefolia)] or in spreading shrubs such as blackberry, mountain laurel (Kalmia latifolia), spicebush (Lindera benzoin), and azalea (Rhododendron spp.). A dense stand of saplings creates a more closed canopy that would inhibit the shrubby growth used by Indigo Buntings and Eastern Towhees for nesting, further indicating that not all types of early successional habitat are equally suitable for bird species considered early successional (Bell and Whitmore 1997b). Although Acadian Flycatchers used saplings for nesting, their nest patches also had significantly fewer sapling trees than surrounding habitat. Acadian Flycatchers prefer areas with a more open understory (Johnston 1970, Gates and Giffen 1991), possibly because of their aerial foraging (Ehrlich et al. 1988) or aerial nest defense (Wilson and Cooper 1998a). This species declined after gypsy moth outbreak (Bell 1997), possibly because of increased numbers of small trees in the mesic habitat they preferred. That Acadian Flycatchers choose nest sites with fewer small trees lends support to the idea that increased understory cover may have made the area less suitable for Acadian Flycatchers. It is possible that their numbers decreased because of the presence of gaps in the canopy, although no differences were found in the amount of canopy cover or the largest live trees and snags between nest plots and random plots in similar habitat.

Habitat features related to the probability of parasitism and predation differed among the four species we examined. Our results suggest that species should not be pooled when examining the probability of parasitism and predation associated with habitat (see also Brittingham and Temple 1996). Even species with seemingly similar nest sites, such as Eastern Towhees and Indigo Buntings showed differences in habitat features related to predation and parasitism; pooling might mask these differences.

It is possible that landscape factors may influence success rates more than defoliation induced habitat changes. According to U.S. Forest Service FIA (Forest Inventory and Analysis) data, Morgan and Berkeley counties in West Virginia, where the Sleepy Creek WMA is located, are approximately 62% forested cover. Areas near Sleepy Creek and Third Hill mountains are even more densely forested. The study plots, although located in a large forested tract, are situated near the periphery of the Sleepy Creek WMA. While they are in the forest interior (> 250 m from edge, based on Robinson et al. 1995), they are within 1.7-7.0 km of agricultural land and human development; cowbirds were heard in the vicinity of all the study plots. Parasitism rates for the species we studied at Sleepy Creek WMA are generally lower than has been reported elsewhere (Walkinshaw 1961, 1966; Brittingham and Temple 1983; Burhans 1997; Suarez et al. 1997; Wilson and Cooper 1998b); however, this may be in part a reflection of a trend for lower parasitism in the East (Hoover and Brittingham 1993). It may also be due to the relatively high percentage of forest cover in the region and closely surrounding the study area, as well as the large size of the study area. Predation and parasitism results at Sleepy Creek were similar to what Robinson and coworkers (1995) found for sites in the Midwest with surrounding forest cover of 60-80%. The exceptions are that Indigo Buntings at Sleepy Creek had slightly higher percent parasitism than was found for heavily forested areas in the Midwest (Robinson et al. 1995). Wood Thrushes had slightly higher daily predation rates and slightly lower percent parasitism and Acadian Flycatchers had lower daily predation rates. The Mayfield nest success rate for Indigo Buntings at Sleepy Creek WMA was higher than was found in riparian habitat in Iowa (Best and Stauffer 1980), and was comparable to that found in several types of gradual edge habitat (stream openings, selection cuttings) in southern Illinois (Suarez et al. 1997). In treefall gaps Suarez and coworkers (1997) reported higher Mayfield nest success in addition to higher percent parasitism for lndigo Buntings than we found, even though all Indigo Bunting nests at Sleepy Creek WMA were in canopy gaps. The Mayfield success rate for Wood Thrushes at Sleepy Creek WMA was lower than rates reported by Hoover and coworkers (1995) for large forested tracts (>100 ha), and comparable to what they found in smaller forest fragments (< 80 ha). However, nesting success of Wood Thrushes in Great Smoky Mountains National Park (Farnsworth and Simons 1999) was found to be similar to what we found at Sleepy Creek WMA. Without data on nesting success prior to defoliation, we are unable to determine if success rates or percent parasitism changed after defoliation.

Tree mortality ranged from approximately 0% to greater than 70% at stands within the study site, with losses on the average of 40% (Bell 1997). Tree losses greater than 50% are considered catastrophic, but generally only 10-15% of infested stands have such high tree mortality (Gottschalk 1991). Considering that losses of less than 20% are most common (Gottschalk 1991), gypsy moth defoliation is not likely to be a devastating ecological event for shrub and sub-canopy nesting species. In light of evidence that many species of birds that use early-successional habitat are declining (Hagan et al. 1992, Hagan 1993, Litvitis 1993, Askins 1995), gypsy moth defoliation and concomitant tree mortality might be useful in creating more nesting habitat for many species that use shrubs and small trees.

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LITERATURE CITED

- ANDERSON, W. L. AND R. W. STORER. 1976. Factors affecting Kirtland's Warbler nesting success. Jack-Pine Warbler 54:105–114.
- ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. Curr. Ornith. 7:1–57.
- ASKINS, R. A. 1995. Hostile landscapes and the decline of migratory songbirds. Science 267:1956– 1957.
- BARBER, D. R. AND T. E. MARTIN. 1997. Influence of alternate host densities on Brown-headed Cowbird parasitism rates in Black-capped Vireos. Condor 99:595–604.
- BELL, J. L. 1997. Effects of gypsy moth defoliation on forest vegetation and a forest bird community. Ph.D. diss., West Virginia Univ., Morgantown.
- BELL, J. L. AND R. C. WHITMORE. 1997a. Bird populations and habitat in *Bacillus thuringiensis* and Dimilin treated and untreated areas of hardwood forest. Am. Midl. Nat. 137:239–250.
- BELL, J. L. AND R. C. WHITMORE. 1997b. Eastern Towhee population increase following defoliation by the gypsy moth. Auk 114:708–716.
- BEST, L. B. AND D. F. STAUFFER. 1980. Factors affecting nesting success in riparian bird communities. Condor 82:149–158.
- BRITTINGHAM, M. C. AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? Bioscience 33:31–35.
- BRITTINGHAM, M. C. AND S. A. TEMPLE. 1996. Vegetation around parasitized and non-parasitized nests within deciduous forest. J. Field Ornith. 67:406– 413.
- BURHANS, D. E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. Condor 99:866–872.
- BUTLER, L., G. A. CRISLIP, V. A. KONDO, AND E. C. TOWNSEND. 1997. Effect of diflubenzuron on nontarget eanopy arthropods in closed, deciduous watersheds in a central Appalachian forest. J. Econ. Ent. 90:784–794.
- CAMPBELL, R. W. AND R. J. SLOAN. 1977. Forest stand responses to defoliation by the gypsy moth. For. Sci. Monog. 19:1–34.
- COOPER, R. J., K. M. DODGE, P. J. MARTINAT, S. B. DONAHOE, AND R. C. WHITMORE. 1990. Effect of diflubenzuron application on eastern deciduous forcst birds. J. Wildl. Manage. 54:486–493.
- COOPER, R. J., K. M. DODGE, D. K. THURBER, R. C. WHITMORE, AND H. R. SMITH. 1993. Response of ground-level wildlife food plants to canopy defoliation by the gypsy moth. Proc. Ann. Conf. Southeast. Assoc. Fish Wildl. Agencies 47:268– 275.
- COOPER, R. J., G. A. GALE, AND L. A. BRENNAN. 1999. Answering questions in management and research using large-scale manipulative experiments. Pp. In Strategies for bird conservation: the Partners in Flight planning process (R. Bonney, D. N. Pash-

ley, R. J. Cooper, and L. Niles, Eds.). Cornell Univ. Press, Ithaca, New York.

- DICKSON, J. G., R. N. CONNER, AND J. H. WILLIAMSON. 1983. Snag retention increases bird use of a clearcut. J. Wildl. Manage. 47:799–804.
- EHRLICH, P. R., D. S. DOBKIN, AND D. WHEYE. 1988. The birder's handbook. Simon and Schuster, Inc., New York.
- FARNSWORTH, G. L. AND T. R. SIMONS. 1999. Factors affecting nesting success of Wood Thrushes in Great Smoky Mountains National Park. Auk 116: 1075–1082.
- GATES, J. E. AND N. R. GIFFEN. 1991. Neotropical migrant birds and edge effects at a forest-stream ecotone. Wilson Bull. 103:204–217.
- GOTTSCHALK, K. W. 1991. Gypsy moth:impacts and silvicultural options. Pp. 159–169 *in* Proceedings of the oak resource in the upper Midwest. Implications for management (S. B. Laursen and J. F. DeBoe, Eds.). Minnesota Extension Service. Minneapolis.
- HAGAN, J. M. 1993. Decline of the Rufous-sided Towhee in the eastern United States. Auk 110:863– 874.
- HAGAN, J. M., T. L. LLOYD-EVANS, J. L. ATWOOD, AND D. S. WOOD. 1992. Long-term changes in the migratory landbirds in the northeastern United States: evidence from migration capture data. Pp. 115–130 in Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- HOLMES, R. T., R. P. MARRA, AND T. W. SHERRY. 1996. Habitat-specific demography of breeding Blackthroated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. J. Anim. Ecol. 65:183–195.
- HOOVER, J. P. AND M. C. BRITTINGHAM. 1993. Regional variation in cowbird parasitism of Wood Thrushes. Wilson Bull. 105:228–238.
- HOOVER, J. P., M. C. BRITTINGHAM, AND L. J. GOOD-RICH. 1995. Effects of forest patch size on nesting success of Wood Thrushes. Auk 112:146–155.
- HOSMER, D. W. AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley, New York.
- HOUSTON, D. R. AND H. T. VALENTINE. 1977. Comparing and predicting forest stand susceptibility to gypsy moth. Can. J. For. Res. 7:447–461.
- HUNT, P. D. 1996. Habitat selection by American Redstarts along a successional gradient in northern hardwoods forest: evaluation of habitat quality. Auk 113:875–888.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187–211.
- JAMES, F. C. AND H. H. SHUGART. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651– 661.

- JOHNSON, R. G. AND S.A. TEMPLE. 1990. Nest predation and brood parasitism of tallgrass prairie birds. J. Wildl. Manage. 54:106–111.
- JOHNSTON, R. F. 1970. High density of birds breeding in a modified deciduous forest. Wilson Bull. 82: 79–82.
- KUPPER, L. L., J. R. STEWART, AND K. A. WILLIAMS. 1976. A note on controlling significance levels in stepwise regression. Am. J. Epidemiol. 103:13–15.
- LIEBHOLD, A. M. 1990. Etienne Leopold Trouvelot, gypsy moth perpetrator. Newslett. Mich. Ent. Soc. 35:1–2.
- LIEBHOLD, A. M., K. W. GOTTSCHALK, R.-M. MUZIKA, M. E. MONTGOMERY, R. YOUNG, K. O'DAY, AND B. REILLY. 1995. Suitability of North American tree species to the gypsy moth: a summary of field and laboratory tests. USDA For. Serv. Gen. Tech. Rep. NE-211:1–34.
- LITVAITIS, J. A. 1993. Response of early successional vertebrates to historic changes in land use. Conserv. Biol. 7:866–873.
- MARTIN, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pp. 455–473 in Ecology and conservation of Neotropical migrant landbirds (J. Hagan and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- MARTIN, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. Bioscience 43: 523–532.
- MARTIN, T. E., C. R. PAINE, C. J. CONWAY, W. M. HO-CHACHKA, P. ALLEN, AND W. JENKINS. 1996. Breeding biology research and monitoring database (BBIRD) field protocol. Montana Cooperative Wildlife Research Unit, Univ. of Montana, Missoula.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.
- MENARD, S. 1995. Applied logistic regression analysis. Sage Univ., Thousand Oaks, California.
- RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook of field methods for monitoring landbirds. U.S.D.A. For. Serv. Gen. Tech. Rep. PSW-GTR-144:1–41.
- ROBBINS, C. S. 1979. Effects of forest fragmentation on bird populations. U.S. For. Serv. Gen. Tech. Rep. NC-51:198–213.
- ROBBINS, C. S., J. R. SAUER, R. S. GREENBERG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Ncotropics. Proc. Nat. Acad. Sci. USA. 86:7658–7662.
- ROBINSON, S. K., F. R. THOMPSON, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.
- RODENHOUSE, N. L. AND R. T. HOLMES. 1992. Results of experimental and natural food reductions for

breeding Black-throated Blue Warblers. Ecology 73:357–372.

- ROTENBERRY, J. T., R. J. COOPER, J. M. WUNDERLE, AND K. G. SMITH. 1995. When and how arc populations limited? The roles of insect outbreaks, fire, and other natural perturbations. Pp. 55–84 in Ecology and management of Neotropical migratory birds (T. E. Martin and D. M. Finch, Eds.). Oxford Univ. Press, Inc., New York.
- SAMPLE, B. E., R. J. COOPER, AND R. C. WHITMORE. 1993a. Dietary shifts among songbirds from a diflubenzuron-treated forest. Condor 95:616–624.
- SAMPLE, B. E., L. BUTLER, AND R. C. WHITMORE. 1993b. Effects of an operational application of Dimilin on non-target insects. Can. Ent. 125:173– 179.
- SAMPLE, B. E., L. BUTLER, C. ZIVKOVICH, R. C. WHIT-MORE, AND R. REARDON. 1996. Effects of *Bacillus thuringiensis* Berliner var. *Kurstaki* and defoliation by the gypsy moth [*Lymantria dispar* (L.) (Lepidoptera:Lymantriidae)] on native arthropods in West Virginia. Can. Ent. 128:573–592.
- SAS INSTITUTE, INC. 1995. Logistic regression examples using the SAS system, version 6. SAS Institute Inc., Cary, North Carolina.
- SAS INSTITUTE, INC. 1996. The SAS system, version 6.12. SAS Institute Inc., Cary, North Carolina.
- SUAREZ, A. V., K. S. PFENNIG, AND S. K. ROBINSON. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. Conserv. Biol. 11:928–935.
- THURBER, D. K., W. R. MCCLAIN, AND R. C. WHIT-MORE. 1994. Indirect effects of gypsy moth defoliation on nest predation. J. Wildl. Manage. 58: 493–500.
- TWERY, M. J. 1991. Effects of defoliation by gypsy moth. U.S. For. Serv. Gen. Tech. Rep. NE-146: 27-39.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893– 901.
- VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992. Is density an indicator of breeding success? Auk 109:706–710.
- WALKINSHAW, L. H. 1961. The effect of parasitism by the Brown-headed Cowbird on *Empidonax* flycatchers in Michigan. Auk 78:266–268.
- WALKINSHAW, L. H. 1966. Studies of the Acadian Flycatcher in Michigan. Bird-Banding 37:227–257.
- WHITMORE, R. C., R. J. COOPER, AND B. E. SAMPLE. 1993. Bird fat reductions in forests treated with Dimilin. Env. Toxicol. Chem. 12:2059–2064.
- WILSON, R. R. AND R. J. COOPER. 1998a. Acadian Flycatcher nest placement: does placement influence reproductive success? Condor 100:673–679.
- WILSON, R. R. AND R. J. COOPER. 1998b. Breeding biology of Acadian Flycatchers in a bottomland hardwood forest. Wilson Bull. 110:226–232.
- YAHNER, R. H. AND A. L. WRIGHT. 1985. Depredation on artificial ground nests: effects of edge and plot age. J. Wildl. Manage. 49:508–513.